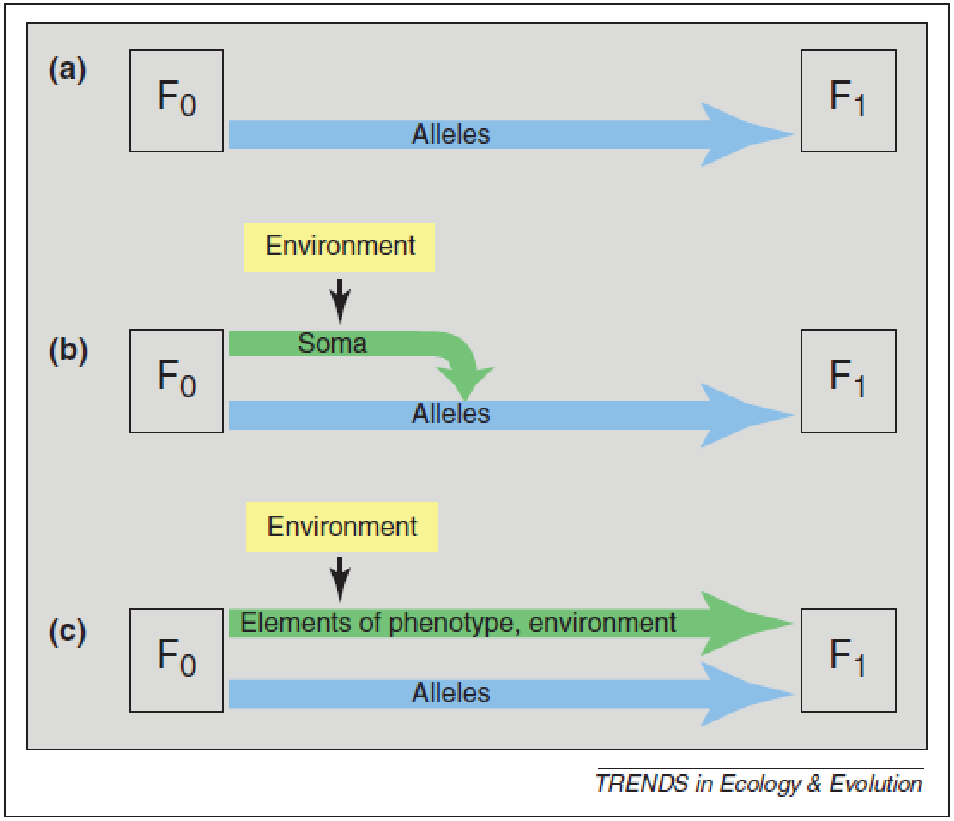
PLURALISTIC HEREDITY



Tom Van Dooren 11/2012
vandoore@biologie.ens.fr

PRICE EQUATION

PRICE EQUATION PARTITIONS

PLURALISTIC HEREDITY

EPIGENETICS

♣ A lecture on topics which were until recently considered to be mostly nonsense and only meaningful for theoreticians

PRICE EQUATION

We include/inspect every individual/entity in the population.

We are not drawing random samples from a population and describing these.

In this manner, the Price equation is exact.

Expressions from statistics are used because the equations match.

Expectation of a random variable E(), *covariance* Cov()

PRICE EQUATION

A (finite) parental population with size N and elements indexed i, elements i have property/trait z_i. each individual represents fraction $q_i = 1/N$ of the population

↓

A population with decendants of the elements i
descendants of i represent a fraction q'_i of the population with property z'_i.

♣ z'_i is the average value of the trait among the descendants of type i

$E[z_i] = \sum_i q_i z_i$ average of z over the entire parental population

$$\downarrow$$

$E[z'_i] = \sum_i q'_i z'_i$ average of z over the entire descendant population

$$E[z'_i] - E[z_i]$$

the difference in average trait value between descendant and parental populations

$$E[z'_i] - E[z_i]$$

$$\sum_i q'_i z'_i - \sum_i q_i z_i$$

$$q'_i = q_i w_i \text{ and } z'_i = z_i + \Delta z_i$$

$$\sum_i q_i w_i (z_i + \Delta z_i) - \sum_i q_i z_i$$

$$= \sum_i q_i (w_i - 1) z_i + \sum_i q_i w_i \Delta z_i$$

$$E[z'_i] - E[z_i] = E[(w_i - 1) z_i] + E[w_i \Delta z_i]$$

$$\Delta \mu_z = Cov[w_i, z_i] + E[w_i \Delta z_i]$$

$$\Delta\mu_z = Cov[w_i, z_i] + E[w_i \Delta z_i]$$

the change in the average trait value
between parental and descendant population

is the sum of the covariance between "fitness" and the trait and

the expectation of the product of fitness and
(expected) trait change per i

$$\Delta\mu_z = S + E[w_i \Delta z_i]$$

S the average trait value "after" - average trait value before selection

Only selection among the parents: S is the selection differential of z

alternative ways of grouping terms:

$$\Delta\mu_z = Cov[w_i, z_i] + E[w_i \Delta z_i]$$

$$\Delta\mu_z = Cov[w_i, z_i] + Cov[w_i, \Delta z_i] + E[\Delta z_i]$$

$$\Delta\mu_z = Cov[w_i, z'_i] + E[\Delta z_i]$$

This last one has a clean separation with fitness variation and transmission in separate terms. To be preferred.

RECOVERING THE BREEDERS EQUATION

partial covariance between *w* and *z*′, controlling for *z*:

$$Cov[w_i, z'_i | z_i]$$

covariance between the residuals of *w* and of *z*' after each has been regressed independently on *z*

$$Cov[w_i, z'_i | z_i] = Cov\left[\varepsilon_i^w, \varepsilon_i^{z'}\right]$$

$$Cov[\varepsilon_i^w, \varepsilon_i^{z'}] = Cov[w_i - 1 - \beta_{w,z} z_i, z'_i - \mu_{z'} - \beta_{z',z} z_i]$$

$$= Cov\left[w_i, z'_i\right] - \beta_{w,z} Cov[z_i, z_i] - \beta_{z',z} Cov[w_i, z_i] + \beta_{z',z}\beta_{w,z} Cov[z_i, z_i]$$

$$= Cov\left[w_i, z'_i\right] - \beta_{z',z} Cov[w_i, z_i]$$

$$Cov[w_i, z'_i | z_i] = Cov\left[w_i, z'_i\right] - \beta_{z',z} S$$

$$\Delta\mu_z = \beta_{z',z} S + Cov[w_i, z'_i | z_i] + E[\Delta z_i]$$

RECOVERING THE BREEDERS EQUATION

$$\Delta\mu_z = \beta_{z',z} S + Cov[w_i, z'_i | z_i] + E[\Delta z_i]$$

$\beta_{z',z}$ is called "biometric heritability"

z' are regressed in the presence of differences among w_i: "after selection"

In many experiments which estimate heritabilities, selection is avoided as much as possible. How can we deal with that?

RECOVERING THE BREEDERS EQUATION

We partition the change between parent and descendants into a reference, the expectation if there would be no selection going on, plus a deviation.

$$z'_i = z^0{}_i + \delta_i$$

$$\beta_{z',z} Cov[w_i, z_i] = \beta_{z^0,z} Cov[w_i, z_i] + Cov[\delta_i, z_i] Cov[w_i, z_i] / Cov[z_i, z_i]$$

$$Cov[w_i, z'_i | z_i] \\ = Cov\left[w_i, z_i^0 | z_i\right] + Cov[w_i, \delta_i] - Cov[\delta_i, z_i] Cov[w_i, z_i] / Cov[z_i, z_i]$$

$$\Delta z_i = \delta_i + z_i^0 - z_i$$

substitute this all

$$\Delta\mu_z = \beta_{z^0,z} S + Cov\left[w_i, z_i^0 | z_i\right] + Cov[w_i, \delta_i] + E[\delta_i] + E[z_i^0 - z_i]$$

heritability estimated across an interval with selection

$$\Delta\mu_z = \beta_{z',z} S + Cov\left[w_i, z_i^0 | z_i\right] + Cov[w_i, \delta_i | z_i] + E[\delta_i] + E[z_i^0 - z_i]$$

using

$$Cov[w_i, \delta_i | z_i] = Cov[w_i, \delta_i] - Cov[\delta_i, z_i] Cov[w_i, z_i] / Cov[z_i, z_i]$$

All terms have gotten names (Heywood 2005)

$\beta_{z',z}S$ linear response to selection

$Cov\left[w_i, z_i^0|z_i\right]$ spurious response to selection

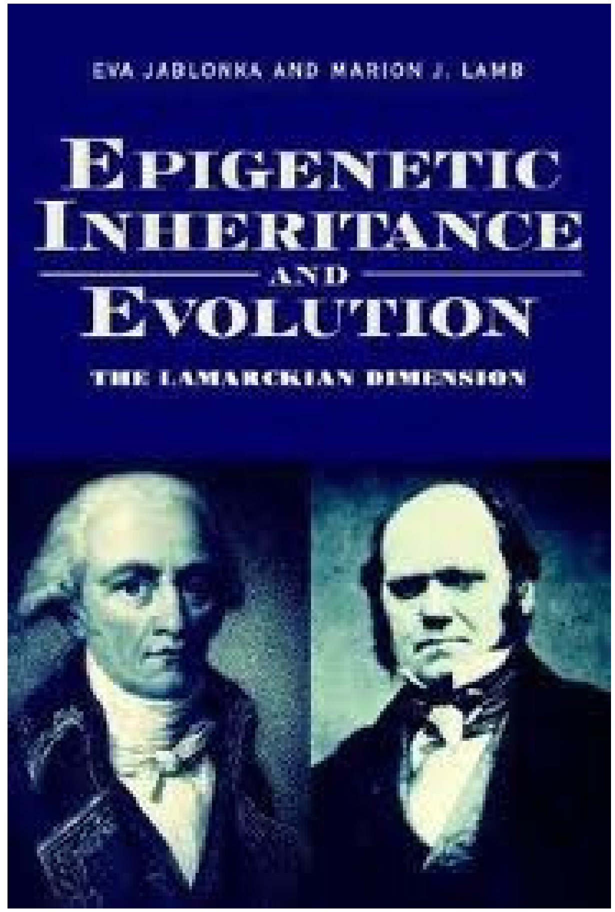
$Cov[w_i, \delta_i|z_i]$ special induced transmission bias

$E[\delta_i]$ general induced transmission bias

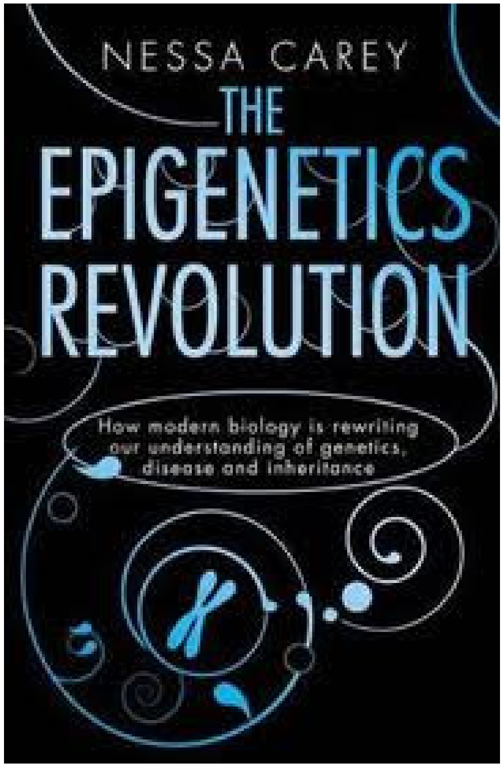
$E[z_i^0 - z_i]$ constitutive transmission bias

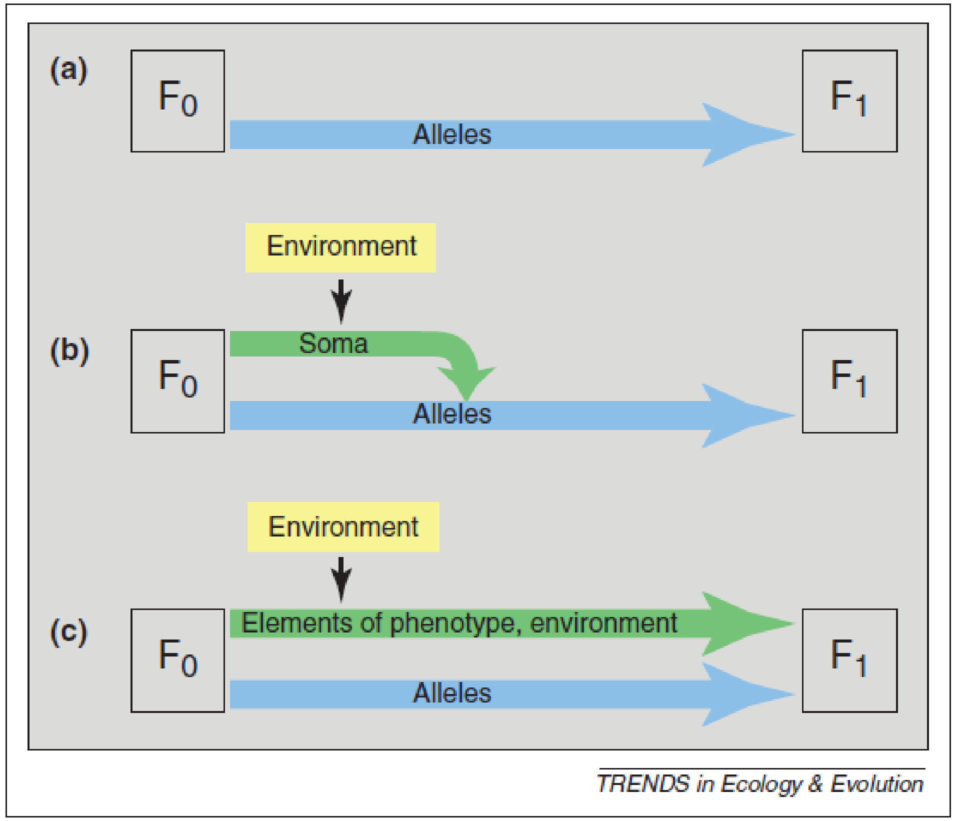
but let's inspect them again and avoid terms like "spurious" and "special"

$\beta_{z',z}S$	selection	linear
$Cov\left[w_i, z_i^0 \middle| z_i\right]$	selection	correction
$Cov[w_i, \delta_i \| z_i]$	selection x transmission	correction
$E[\delta_i]$	selection x transmission	bias
$E[z_i^0 - z_i]$	transmission	bias


EVA JABLONKA AND MARION J. LAMB
EPIGENETIC
INHERITANCE
AND
EVOLUTION
THE LAMARCKIAN DIMENSION


DER SPIEGEL
DER SIEG ÜBER DIE GENE
Klüger, gesünder, glücklicher: Wie wir unser Erbgut überlisten können


NESSA CAREY
THE EPIGENETICS REVOLUTION
How modern biology is rewriting our understanding of genetics, disease and inheritance


(a)
F0
Alleles
F1
Environment
(b)
F0
Soma
Alleles
F1
Environment
(c)
F0
Elements of phenotype, environment
Alleles
F1
TRENDS in Ecology & Evolution

track changes in genotypic values *g* and epigenetic state *h* across an interval.

$$\Delta\mu_g = Cov[w_i, g_i] + E[w_i \Delta g_i]$$

$$\Delta\mu_h = Cov[w_i, h_i] + E[w_i \Delta h_i]$$

approximate fitness as

$$w(g, h, \bar{g}, \bar{h}) = 1 + \left.\frac{\partial w}{\partial g}\right|_{g=\bar{g}, h=\bar{h}} (g - \bar{g}) + \left.\frac{\partial w}{\partial h}\right|_{g=\bar{g}, h=\bar{h}} (h - \bar{h})$$

$$\Delta\mu_g = Cov[g,g]\left.\frac{\partial w}{\partial g}\right|_{g=\bar{g},h=\bar{h}} + Cov[g,h]\left.\frac{\partial w}{\partial h}\right|_{g=\bar{g},h=\bar{h}} + E[w\Delta g]$$

$$\Delta\mu_h = Cov[g,h]\left.\frac{\partial w}{\partial g}\right|_{g=\bar{g},h=\bar{h}} + Cov[h,h]\left.\frac{\partial w}{\partial h}\right|_{g=\bar{g},h=\bar{h}} + E[w\Delta h]$$

Direct and indirect selection - Interactions + Transmission effects

Examples

Maternal effects: offspring inherit the nongenetic value $m(g+h)$ of the parent

$$\Delta\mu_g = Cov[g,g]\left.\frac{\partial w}{\partial g}\right|_{g=\bar{g},h=\bar{h}} + Cov[g,h]\left.\frac{\partial w}{\partial h}\right|_{g=\bar{g},h=\bar{h}}$$

$$\Delta\mu_h = Cov[g,h]\left.\frac{\partial w}{\partial g}\right|_{g=\bar{g},h=\bar{h}} + Cov[h,h]\left.\frac{\partial w}{\partial h}\right|_{g=\bar{g},h=\bar{h}}$$

$$+mE[wg] + (m-1)E[wh]$$

Day and Bonduriansky (2011)

Epialleles: methylated and unmethylated states (h = 0/1)

$$\Delta\mu_g = Cov[g,g]\left.\frac{\partial w}{\partial g}\right|_{g=\bar{g},h=\bar{h}} + Cov[g,h]\left.\frac{\partial w}{\partial h}\right|_{g=\bar{g},h=\bar{h}}$$

$$\Delta\mu_h = Cov[g,h]\left.\frac{\partial w}{\partial g}\right|_{g=\bar{g},h=\bar{h}} + Cov[h,h]\left.\frac{\partial w}{\partial h}\right|_{g=\bar{g},h=\bar{h}}$$

$$+(rate\ of\ epigenetic\ change)(relative\ rate\ of\ methylation - relative\ rate\ of\ demethylation)$$

Day and Bonduriansky (2011)

References

Day T, Bonduriansky R. 2011. A unified approach to the evolutionary consequences of genetic and nongenetic inheritance. Am Nat 178:E18–E36

Frank, S. A. 1997. The Price Equation, Fisher's fundamental theorem, kin selection, and causal analysis. Evolution 51:1712-1729.

Heywood JS. 2005. An exact form of the breeder's equation for the evolution of a quantitative trait under natural selection. Evolution 59(11): 2287-98

Okasha. S. Evolution and the Levels of Selection. Oxford University Press.